VARIATION IN LINEAR DIMENSIONS, TEST WEIGHT AND AMBULACRAL PORES IN THE SAND DOLLAR, ECHINARACHNIUS PARMA (LAMARCK)[1]

PRASERT LOHAVANIJAYA[2]

Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824

That the regular sea urchins have considerable variation in respect to a number of meristic and mensural characteristics has long been recognized. In varying degrees Jackson (1912, 1914, 1927), Kongiel (1938), Vasseur (1952), and Swan (1962) have studied this variation and suggested that at least some of it might be either environmentally induced or selected. Kongiel also applied his methods of analysis to fossil remains of heart urchins, and Kermack (1954) and Nichols (1959a, 1959b, 1962) have more recently extended this work. Durham (1955) in his monumental "Classification of Clypeasteroid Echinoids" has indicated that in the sand dollars there is a great deal of variation, and Raup (1958) has gathered evidence that in the Pacific Coast sand dollar, *Dendraster excentricus* (Eschscholtz), heavier tests are characteristic of populations from colder water.

In the present paper findings and suggested possible causal relationships with environmental factors are presented for *Echinarachnius parma* (Lamarck), based on collections from several localities in New England on the Atlantic Coast. The characteristics studied are (1) the relationship between length and width of the test, (2) test weight at comparable sizes, and (3) the numbers of pore-pairs in the petaloid areas of the aboral surface of the test. This material extends some of Durham's (1955) findings and is suggestive of the need for carefully designed statistical studies of variation in this species and for experimental studies on the effects of differing environmental factors on its growth pattern.

Materials and Methods

Collections

Six series of sand dollars were collected intertidally, either by hand, or with the aid of a rake. A series of specimens was taken from each of the following places: Crow Neck, North Trescott, Washington County, Maine (44° 52′ 37″ N, 67° 07′ 38″ ±10″ W); Bailey's Mistake, South Lubec, Washington County, Maine (44° 46′ 23″ N, 67° 03′ 16″ W); Paradise Point, Boothbay, Lincoln County, Maine (43° 51′ N, 69° 35′ W); Hampton Beach, Rockingham County, New Hampshire (42° 54′ 07″ N, 70° 48′ 40″ W); Hampton Harbor, Rockingham County, New Hampshire (42° 53′ 59″ N, 70° 49′ 07″ W); and Scusset Beach, Barnstable County, Cape Cod, Massachusetts (41° 47′ 18″ N, 70° 30′ 30″ W).

[1] This work represents a portion of a dissertation submitted to the University of New Hampshire in partial fulfillment of the requirements for the Ph.D. degree.

[2] Present address: New England College, Henniker, New Hampshire.

The total number of specimens collected from these six areas was 1696. Two additional series, from New Castle, Rockingham County, New Hampshire (43° 03′ 22″ N, 70° 44′ 17″ W) and Eastern Point, Gloucester, Essex County, Massachusetts (42° 35′ 00″ N, 70° 40′ 00″ W) were collected subtidally. At New Castle a skindiver made the collection from about 5 feet of water while at Gloucester the animals were obtained with a rake over the side of a rowboat. The total number of specimens collected from these two localities was 519. The animals were preserved in 10% formalin in fresh water for 24–72 hours and then dried at room temperature before being measured.

The rake was purchased as a steel garden rake 14 inches wide and about 4 inches high at the opening, with two-inch teeth spaced one inch apart along the lower side of the opening. The handle, 5 feet in length, was made of wood. Hardware cloth (¼-inch mesh) was used to construct a basket, 14 inches deep,

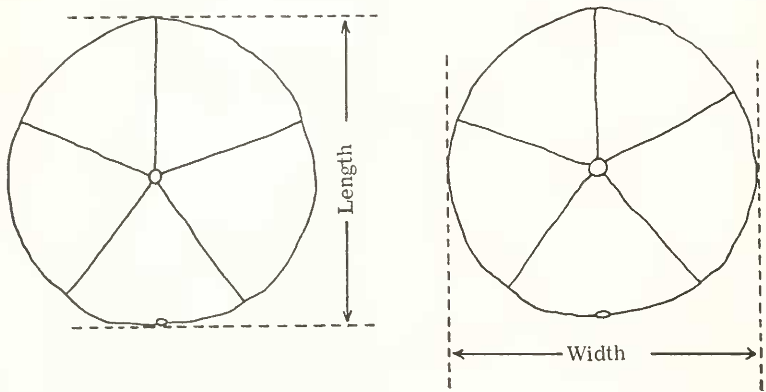

FIGURE 1. Diagrammatic oral surface of the sand dollar, *Echinarachnius parma*, showing length and width of the test.

which was fastened to the opening between the bow and the rake proper. This basket was attached by means of wire.

Method of measuring

A vernier caliper calibrated on the main scale in millimeters and on the vernier to tenths was used for all the measurements. The spines were removed from those portions of the test where contact with the calipers was to be made.

Length

The distance from the edge where the anus is located to the opposite edge of the animal is considered the length of the test (Fig. 1).

Width

The width of the test is obtained by measuring the distance from side to side, perpendicular to that of the length (Fig. 1).

Average diameter

½ (Length + Width), as used by Durham (1955), has been used as the basic criterion of the animals' size.

Variation in Relative Linear Dimensions

The specimens of each series were measured to the nearest tenth of a millimeter for length and width. The resulting data were tabulated into groups for each 5-mm. interval of mean test diameter, ½ (Length + Width). The numbers of specimens longer than wide, having length equal to width, and wider than long have been tallied. Tallies for all eight series were prepared. A summary of these data for all the series, but without reference to size of individuals, is given in Table I. The data tabulated according to size group show no appreciable change in relationship with size. Mean dimensions for the four chief series divided into size groups are plotted in Figure 2.

Table I

Relative lengths and widths of specimens from different localities

Locality	Numbers of specimens			
	Longer	Wider	L = W	Total
Hampton Harbor, N. H.	117 (37.6%)	176 (56.6%)	18 (5.9%)	311
Hampton Beach, N. H.	11 (3.0%)	358 (96.5%)	2 (0.5%)	371
Bailey's Mistake, Maine	23 (7.5%)	282 (92.2%)	1 (0.3%)	306
Crow Neck, Maine	250 (78.9%)	57 (18.0%)	10 (3.2%)	317
Scusset Beach, Mass.	11 (4.5%)	229 (93.1%)	6 (2.4%)	246
New Castle, N. H.	53 (29.4%)	121 (67.2%)	6 (3.3%)	180
Boothbay Harbor, Maine	81 (55.9%)	55 (37.9%)	9 (6.2%)	145
Gloucester, Mass.	112 (32.6%)	211 (61.3%)	21 (6.1%)	344

Examination of these data reveals that the populations from Hampton Beach, New Hampshire, and those from Bailey's Mistake, Maine, have more wider than longer individuals and average wider than long more markedly than is the case for any of the other collections. In distinct contrast to these collections is the one from Crow Neck, Maine, whose members tend to be longer than wide. The collections from the other five localities fall well between these extremes.

Comparisons of the mean dimensions of these five collections (Hampton Harbor, New Hampshire; Boothbay Harbor, Maine; New Castle, New Hampshire; Gloucester, Massachusetts; and Scusset Beach, Massachusetts) reveal that at Scusset Beach the tests grow appreciably wider than long but not as markedly so as at Hampton Beach and Bailey's Mistake. The collection from New Castle averages slightly over 1% wider than long. In none of the other three series (Hampton Harbor, Paradise Point, and Gloucester) is one dimension more than 1% greater than the other dimension. Likewise in none of these series does the ratio of longer to wider specimens deviate from equality beyond 2:1 or 1:2.

The habitat at Crow Neck is unusual. Because it is on the shore of a constricted channel through which large amounts of water pass to and from large inner bays, to the extent of changing their levels many feet on each cycle, it has an almost continuous but reversing flow of water. This resembles a rather swift river which flows nearly six hours in one direction, followed by a brief period of nearly slack water, and then another period of rapid flow in the opposite direction, again for nearly six hours. One would thus expect only rocks and relatively coarse sediments, which are in fact found in the main channels. Most of the sand dollars were found living in eddies which occurred in the small wider parts of the channel. The rather soft sandy substratum under these eddies was generally finer than in the main channels and was often overlain by a layer of mud, silt, or detritus. Thus, the sand dollars living in this habitat live in contact with a

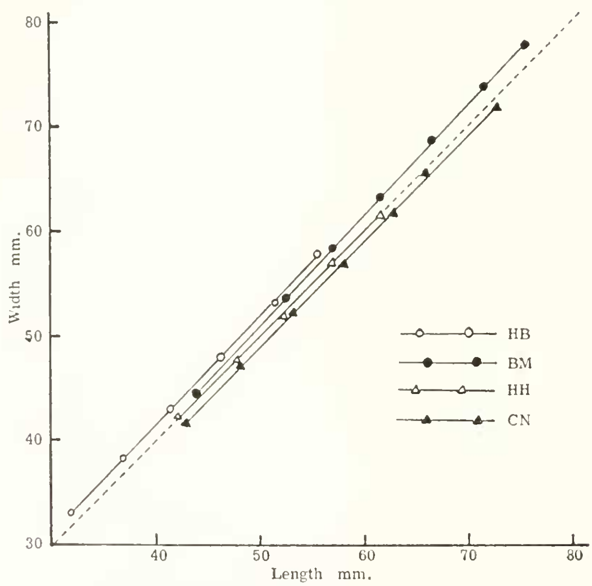

FIGURE 2. Relationship of width to length. HB—Hampton Beach; HH—Hampton Harbor; BM—Bailey's Mistake; CN—Crow Neck.

nearly continuous current but encounter almost no pounding by waves, and the current's direction changes only a few times a day. It appears that they tend to grow longer than wide.

In contrast with the conditions at Crow Neck we find at Hampton Beach and Bailey's Mistake little continuous current and considerable exposure to surf.

At Hampton Beach, particularly, the surf action is considerable almost all the time. Here the sand grains are fine and hard-packed. The situation at Bailey's Mistake is similar to Hampton Beach but there appears to be some reduction in surf action by the headlands to either side of the entrance to the bay, as is made evident by the eel grass growing in the bay, which in turn appears to give the organisms living among it additional protection. The sand dollars that live in these two places (see Fig. 2) appear to grow quite consistently wider than long.

A situation between the continuously running water at Crow Neck and surf at Hampton Beach can be found at Hampton Harbor. It is a protected harbor southwest of the village of Hampton Beach. Since it is protected, it has little surf action. The current, due to the flow in and out of the tide, is appreciable but much less than at Crow Neck. The area where the sand dollars were collected is covered by water most of the time. During extremely low tides it becomes a shallow quiet pool. The substratum is a mixture of sand and mud with much organic matter. From Table I it can be seen that the animals usually grow a little wider than long. However, they are not nearly as wide as those from Bailey's Mistake or from Hampton Beach. This is true both in terms of average dimensions and in terms of the number of individuals wider than long compared with the number longer than wide.

Thus there are three kinds of habitats involved in this study, namely: (1) soft sand substratum and continuous current, (2) substratum with appreciable amounts of mud, probably high in organic matter, under relatively quiet water with little surf action, and (3) hard-packed fine sand, containing no evident mud and probably little organic matter, associated with heavy surf.

These observations suggest significant correlation between the kind of habitat and the usual form of the sand dollars inhabiting these habitats. Whether the differences in habitat influence the growth pattern of the animals or bring about a differential selection from a heterogeneous gene pool has not been determined.

Variation in Test Weight

Ten specimens were picked from each 5-mm. size group from the four main series. The spines of these specimens were removed, and then the tests were weighed in grams to the nearest 0.01 gm. The average weights obtained and the average dimensions of the groups of specimens used from the four localities, Crow Neck, Hampton Harbor, Bailey's Mistake, and Hampton Beach, were tabulated.

Obtaining the real test weight, excluding the spines, the soft parts, and the contents of the digestive tract, is a problem. In order to approach a close approximation to the true test weight, one must remove the spines and then cut the test with a thin saw. Raup (1957) used a diamond saw. Then his specimens were cleaned, dried, and weighed to the nearest 0.1 gm.

After he determined the loss of weight (amounting to about 5% for a specimen 35 mm. in diameter) for 24 of his specimens, he considered it insignificant and disregarded it in his computations.

To determine the loss resulting from the cut and the weight of the soft parts and the gut contents, I selected 10 specimens of approximately the same size (*ca.* 50 mm. in mean diameter) from each of the main series.

The spines were removed and the tests were weighed to the nearest 0.01 gm. They were then cut with a thin electric saw and weighed again. The soft parts and the gut contents, but not the lantern, were removed and the weights were determined once more. The total loss of weight, loss from the cut, and the weight of the soft parts and the gut contents were calculated as percentages in the following manner:

$$\text{The total loss of weight} = \frac{\text{The difference in weight before cutting and after cleaning inside}}{\text{Weight before cutting}} \times 100$$

$$\text{The weight loss from the cut} = \frac{\text{The difference in weight before and after cutting}}{\text{Weight before cutting}} \times 100$$

$$\text{The weight of the soft parts and gut contents} = \frac{\text{The difference in weight after cutting and after cleaning inside}}{\text{Weight before cutting}} \times 100$$

The percentage figures are shown in Table II. It should be noted that the lantern is considered part of the test weight. This is in contrast with Raup's (1957) method.

From Table II we can see that the greatest percentage of total loss in weight was 8.7% from a specimen from Bailey's Mistake and the lowest one was 1.9% from a specimen from Hampton Beach, with a mean of 4.14% for all 40 specimens. The weight of the soft parts and the gut contents ranged from 6.1% down to 0.6% among the 40 specimens. It appears that the weight of the soft parts and the gut contents is of little significance and thus has very little effect on the total weight of the dried animal. However, it is interesting to note that the average percentages of the soft parts and gut contents appear to vary with locality and, rounded to the nearest ½%, amount to 1½%, 2½%, 5%, and 1½% from Crow Neck, Hampton Harbor, Bailey's Mistake and Hampton Beach, respectively. Therefore, in this part of the investigation, the weight of the test used, in each series, was obtained by subtracting this predetermined percentage of weight of the soft parts and the gut contents from the specimen's weight before cutting.

The test weights in grams are tabulated and plotted against mean diameters in Table III and Figure 3. As expected, the weights increase slowly when the animals are small in size and then increase somewhat more rapidly as they become larger. In general it appears that at comparable sizes the specimens from Crow Neck are heaviest and those from Hampton Beach are lightest. The series from Bailey's Mistake and Hampton Harbor are between the extremes, with those from Bailey's Mistake being slightly heavier.

Raup (1958) discussed "The Relation between Water Temperature and Morphology in *Dendraster*," and found the tests of the Pacific sand dollar, *Dendraster excentricus* (Eschscholtz), of a given size to be heavier in cold water than in warm water. He also stated that this correlation is interpreted as the result of phenotypic (nonheritable) adaptation to water temperature. The findings here noted appear to correspond to Raup's ideas. The weights of specimens from Crow Neck and Bailey's Mistake, both from eastern Maine, are heavier than the specimens from Hampton Harbor and Hampton Beach, both from the coast of New Hampshire. According to the "Surface Temperatures at Tide Stations, Atlantic Coast" (U. S. Department of Commerce, 1951), the annual average surface water temperature for Eastport, Maine, from 1944 to 1950 was 44.1° F. and for Portsmouth, New Hampshire, from 1944 to 1950 was 47.4° F. It can

TABLE II

Weight losses incurred by cutting tests and cleaning tests. The deductions from total weights made in Table III are based on these figures

#		Weight			Weight loss %			Ave. soft part & gut contents rounded to nearest ½%
		Before cutting	After cutting	After cleaning inside	Total	Cut	Soft part & gut contents	
CN	121	11.60	11.44	11.33	2.3	1.4	0.9	
	125	9.95	9.75	9.55	4.0	2.0	2.0	
	130	9.15	8.95	8.80	3.8	2.2	1.6	
	135	5.94	5.84	5.71	3.8	1.7	2.1	
	136	11.69	11.52	11.24	3.8	1.5	2.3	1.5%
	137	9.61	9.47	9.36	2.6	1.5	1.1	
	140	9.21	9.10	8.97	2.6	1.2	1.4	
	146	10.10	9.97	9.81	2.9	1.3	1.6	
	152	7.58	7.52	7.38	2.6	0.8	1.8	
	163	8.54	8.43	8.28	3.0	1.3	1.8	
HH	89	7.50	7.30	7.10	5.3	2.7	2.6	
	94	6.90	6.70	6.45	6.5	2.9	3.6	
	115	8.92	8.81	8.60	3.6	1.2	2.4	
	121	7.57	7.48	7.23	4.5	1.2	3.3	
	123	8.16	8.08	7.91	3.1	1.0	2.1	2.5%
	136	8.04	7.92	7.73	3.6	1.5	2.1	
	137	8.17	8.08	7.82	4.3	1.1	3.2	
	154	7.52	7.43	7.24	3.7	1.2	2.5	
	158	7.63	7.54	7.41	2.9	1.2	1.7	
	177	7.64	7.52	7.32	4.2	1.6	2.6	
BM	4	7.45	7.35	6.90	7.4	1.3	6.1	
	5	8.81	8.68	8.21	6.8	1.5	5.3	
	7	7.72	7.64	7.16	7.3	1.0	6.3	
	9	8.01	7.89	7.65	4.5	1.5	3.0	
	10	7.45	7.30	6.80	8.7	2.6	6.1	5%
	12	7.27	7.16	6.78	6.7	1.5	5.2	
	16	6.90	6.81	6.46	6.9	1.3	5.6	
	17	8.94	8.82	8.49	5.0	1.3	3.7	
	19	8.29	8.19	7.78	6.2	1.2	5.0	
	24	7.15	7.06	6.64	7.1	1.3	5.8	
HB	328	7.00	6.80	6.70	4.3	2.9	1.4	
	329	6.22	6.16	6.05	2.7	1.0	1.7	
	334	7.20	7.13	7.06	1.9	1.0	0.9	
	337	6.56	6.50	6.43	2.0	0.9	1.1	
	339	7.07	6.99	6.90	2.4	1.1	1.3	1.5%
	341	5.89	5.83	5.76	2.2	1.0	1.2	
	345	5.08	5.01	4.98	2.0	1.4	0.6	
	346	6.75	6.65	6.50	3.7	1.5	2.2	
	348	4.98	4.92	4.85	2.6	1.2	1.4	
	167	5.82	5.76	5.70	2.1	1.0	1.1	

TABLE III

Mean weights and diameters of specimens. Each average is that of 10 individuals unless a smaller number is indicated in parentheses after the mean diameter figures

Crow Neck		Hampton Harbor		Bailey's Mistake		Hampton Beach	
½ (L + W) mm.	Total wt. −1.5% (soft part) gm.	½ (L + W) mm.	Total wt. −2.5% (soft part) gm.	½ (L + W) mm.	Total wt. −5% (soft part) gm.	½ (L + W) mm.	Total wt. −1.5% (soft part) gm.
14.85 (8)	0.21	—	—		—	—	—
20.99 (7)	0.54	—	—	—	—	21.59	0.61
—	—	—	—	—	—	25.96	0.95
31.24 (7)	1.98	—	—	—	—	30.52	1.53
36.51	3.00		—		—	35.40	2.08
40.64	4.12	41.82	3.90	—	—	40.13	2.77
45.76	6.36	45.48	5.20	—	—	45.21	4.01
51.55	9.20	51.24	7.54	52.00	7.50	51.69	6.17
55.44	11.41	55.30	8.52	55.36	8.67	56.68	7.39
60.52	12.96	60.63	10.91	60.34	11.34	—	—
65.37	15.97	—		65.73	13.70	—	—
72.40 (6)	17.93	—	—	70.72	16.62	—	—
	—	—	—	75.27	18.97	—	—
—		—	—	82.32	23.58	—	—

be seen that the difference in water temperature for this period was 3.3° F. More work needs to be done before any causal relationship can be demonstrated, and the differences found between the two New Hampshire series and between the two Maine series suggest that other factors may be involved.

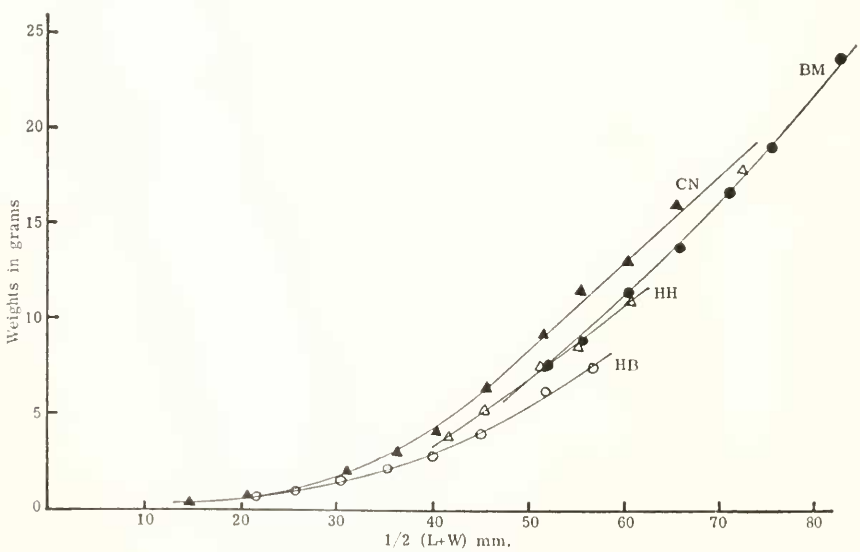

FIGURE 3. Relationship of test weight to size, ½ (L + W).

Variation in Pore-Pairs in Petals

The five smallest specimens of each 5-mm. size group from each of the four main series were used for the counting of pore-pairs in the petaloid areas of the ambulacra. The numbers of pore-pairs in all five petals in each specimen were counted. In order to set up a standard for all specimens, it was necessary to determine the distal limits of the petals. Figure 4 shows that there are two rows of pore-pairs in each, starting at the ambulacral plates nearest the apical system. Near the apex these two rows of pores are close together. Gradually these rows

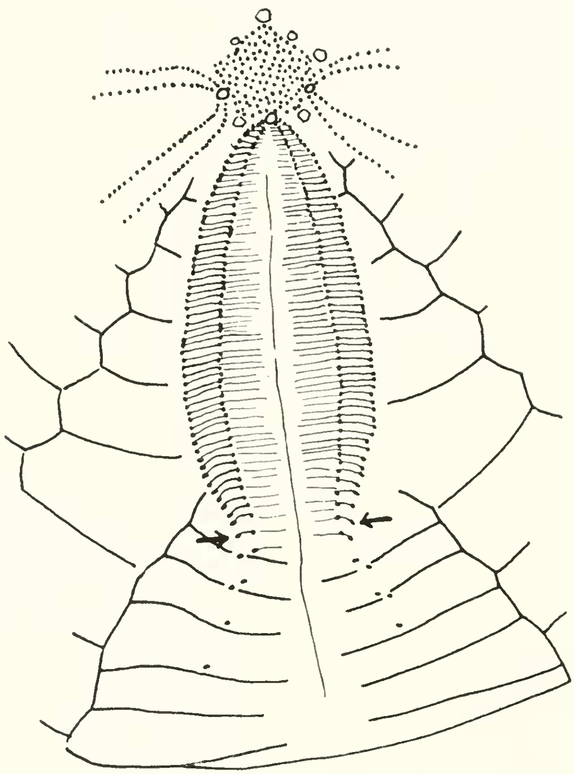

Figure 4. An ambulacral sector of the aboral surface of the sand dollar, *Echinarachnius parma*, showing the arrangement of ambulacral pores in the "petal" of ambulacral area II. The arrows indicate the last pore-pairs to be counted in determining the number of these included in the "petal." Specimen from Boothbay Harbor, Maine (3.1 ×).

of pore-pairs spread apart and then toward the periphery they come closer together again, but remain separated. Thus, in the terminology of students of the irregular urchins (*cf.* Durham, 1955) *Echinarachnius* has "open petals." Beyond the point of this coming together of the rows of pore-pairs, they diverge, and these conspicuous pore-pairs become infrequent. In this investigation counting of pore-pairs has been stopped at the point where the rows start diverging from each other (Fig. 4).

The mean diameters and numbers of pore-pairs in each size group for each series are summarized in Table IV. There are only two common size groups among these four series.

When we compare the four populations and limit our findings to these two common size groups, it is obvious that, in both size groups, the animals from Crow Neck have on the average the smallest number of pore-pairs in the petals. The specimens from Hampton Beach and Hampton Harbor are close together and compete for having the highest numbers of pore-pairs. The Bailey's Mistake specimens show numbers between these extremes. Because of the differences in the size ranges among these series, it is difficult to compare them directly. To minimize this difficulty, a graph showing the relationship of the number of pore-pairs to size, $\frac{1}{2}$ (L + W), has been drawn as Figure 5.

From this graph it is apparent that among these four series, the series from Crow Neck has the lowest number of pore-pairs whereas the Hampton Harbor series has the highest at comparable sizes. The Hampton Beach and Bailey's Mistake series are in between with Hampton Beach being somewhat higher and at some sizes nearly the same as Hampton Harbor. The lines drawn on the graph have been fitted by eye. With the amount of data presently available, it appears doubtful that more careful fitting would be justified.

Durham (1955, p. 87) states that it appears probable that the number of plates inside the petals is a better indication of the age than is the absolute size. If this is true, the sand dollars that live at Crow Neck are growing faster than those

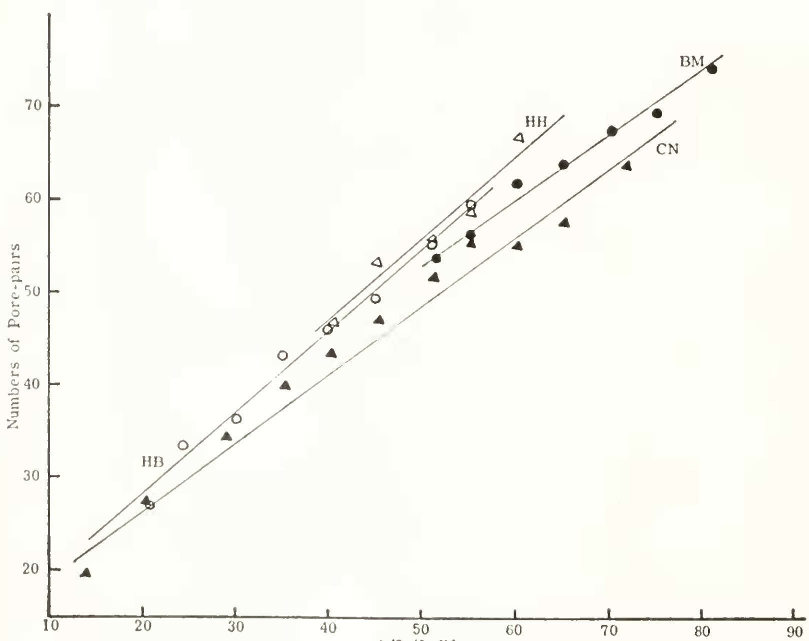

FIGURE 5. Relationship of the number of pore-pairs to size, $\frac{1}{2}$ (L + W).

Table IV

The mean dimensions and pore-pairs. Each average is that of 5 individuals unless a smaller number is indicated in parentheses

Crow Neck		Hampton Harbor		Bailey's Mistake		Hampton Beach	
½ (L + W) mm.	Pore-pairs	½ (L + W) mm.	Pore-pairs	½ (L + W) mm.	Pore-pairs	½ (L + W) mm.	Pore-pairs
13.9	19.6	—	—	—	—	—	—
20.1	27.1	—	—	—	—	20.9	27.6
28.9 (4)	34.4 (4)	—	—	—	—	25.4	33.7
—	—	—	—	—	—	30.2	36.4
35.3	40.4	—	—	—	—	35.2	43.3
40.3	43.9	40.6	46.9	—	—	40.1	46.3
45.4	47.0	45.1	53.3	—	—	45.1	49.5
51.3	51.6	51.2	55.8	51.7	53.9	51.4	55.5
55.3	55.5	55.2	58.8	55.2	56.1	55.5	59.3
60.2	55.0	60.2	66.9	60.2	61.8	—	—
65.1	57.4	—	—	65.3	63.9	—	—
72.0	63.6	—	—	70.4	67.2	—	—
—	—	—	—	75.1	69.1	—	—
—	—	—	—	81.4	74.0	—	—

living in the other localities studied. Also it would appear that the animals from eastern Maine generally grow faster than those from southern New Hampshire.

Discussion

In this study variations among populations of sand dollars (*E. parma*) from different localities have been noted. These variations pertain to relative linear dimensions, test weight, and numbers of pore-pairs in the petals.

The preponderance of relatively longer specimens from Crow Neck, Maine, where they live in what is essentially a reversible tidal river, and the strong tendency for specimens to be wider than long at Hampton Beach, New Hampshire, Bailey's Mistake, Maine, and Scusset Beach, Massachusetts, where they live on surf-swept beaches, suggest that in some way the nature of the water movement where these animals live may affect their shape or bring about a selection such that longer individuals are selected where there are fairly strong currents flowing in one direction for several hours continuously, and wider specimens are selected where there is a mixture of current, often frequently reversing, and with the pounding of breaking waves. The occurrence of populations intermediate in this respect in localities where there is little surf, and what appears to be less current, supports the idea that there is some sort of correlation between the relative linear dimensions of these animals and the nature of the environment in which they live.

That there may be correlations between habitat and relative linear dimensions in other scutellinids is suggested by the literature discussing the status of *Dendraster excentricus* var. *elongatus* H. L. Clark 1935. Clark clearly considers it a variety. Grant and Hertlein (1938) at least tentatively accept Clark's opinion. MacGinitie and MacGinitie (1949) think there are two species which differ in form and habitat requirements. Mortensen (1948) considers this variation not to justify even varietal status. Durham (1955), without mention of the taxonomic question, states (p. 159), "It seems that the excentricity of the apical system and the greater posterior development of the food grooves is correlated with this habit [living on the edge where not too strongly affected by wave action]. The non-excentric species [specimens?] probably lie flat on the sea floor."

Thus, there appears to be a somewhat similar problem among populations of *Dendraster* on the Pacific Coast. Because the varietal name "*elongatus*" applied to the populations living in quiet water suggests that the animals are longer than those typical for the species that live on the surf-swept beaches, it would appear that the correlation between relative linear dimensions and water movement in the habitat is the same in *Dendraster* as in *Echinarachnius*. There is, however, a question concerning what Clark (1935) considers length. He describes the holotype as being 41.5 mm. long and 40 mm. wide, but the specimen the MacGinities (1949) illustrate (Figure 100, page 238) is distinctly wider than long. Thus, the question arises as to whether this discrepancy results from differences in terminology—*i.e.*, what is meant by "length"—or from real differences between Clark's and the MacGinities' concept of the variety. To settle this, Clark's holotype (M.C.Z., No. 6040, not 3343 as Clark says) has been examined and measured. It is in fact longer than wide (41.2 mm. long × 40.5 mm. wide by my measurement) as are the two paratypes (M.C.Z., No. 6041). Thus, one is tempted to suspect that Clark (1935) and the MacGinities (1949) had rather different ideas concerning the characteristics of the variety, and careful reading of Clark's (1935) description and the MacGinities' (1949) discussion tends to substantiate this, not only in terms of shape but also in habitat. Even so it would appear that there is need for careful quantitative work aimed at determining the nature of any causal relationship that may exist between linear dimensions and habitat.

As shown in Table III and Figure 3, there appear to be rather distinct differences in the relationships between test weight and mean diameter. The populations from Crow Neck, Maine, and Hampton Beach, New Hampshire, appear to be at the extremes of the four collections examined, with those from Crow Neck being relatively the heaviest and those from Hampton Beach being the lightest. Again the populations from Bailey's Mistake, Maine, and Hampton Harbor, New Hampshire, are intermediate, with those from Bailey's Mistake appearing to be slightly the heavier, but because of the small amount of overlap in size-range between these two populations, this is a questionable difference. It is possible that whatever factors may be responsible for the differences in relative linear dimensions may also be operating here in respect to the relationship between test-weight and mean diameter. However, it should be recalled that Raup (1958) found the tests of the Pacific sand dollar, *Dendraster excentricus*, to be heavier in relation to diameter in populations from cold water than those from warmer water and that the available data appear to indicate that the mean annual water temperatures for the Maine localities are probably some 3° F. lower than those for the New Hampshire localities. That there may be other factors involved can hardly be doubted. H. L. Clark (1948) in an attempt to find a possible causal basis for explaining differences in numbers of coronal plates in tests of the regular sea urchin, *Strongylocentrotus franciscanus*, of comparable sizes suggests (p. 278) that "unusual features of their habitat, such as excessively strong surf or tidal currents" may affect this relationship. Swan (1962) found that specimens of *S. droebachiensis* living off the Gaspé, from shallower and presumably more turbulent water, had more coronal plates than those from deeper and presumably quieter water. Although I have found no statements in the literature on the subject, Swan in conversation tells me he strongly suspects that the tests of the specimens with relatively more numerous plates are also heavier at comparable sizes. In bivalve mollusks there appears to be a significant amount of evidence (Shih, 1937; Swan, 1952) that, more or less generally, factors that reduce the rate of growth tend to increase shell thickness at comparable sizes. Likewise there is a vast literature (*cf.* Barlow, 1961) indicating that fishes grown under conditions retarding their growth rate through critical stages in their development often have larger numbers of meristic structures. It should, however, always be remembered that the skeletons of the mollusks and the vertebrates differ greatly from each other and from the skeletons of echinoderms. Thus, although similarities may appear great, caution should be used when speculating concerning what might happen in one group on the basis of what has been observed in another. That oxygen content of the water could affect shell or test thickness through its effect on ease of precipitation of $CaCO_3$ should be considered. Finally, the possibility of the selection of different genetic types by different sets of environmental factors cannot be ruled out. Under some conditions it is possible that heavier tests would have distinct survival value whereas under others lighter tests might be advantageous. Nichols' (1962) study of differences between populations of heart urchins (*Echinocardium cordatum* Pennant) should be instructive to anyone trying to determine whether morphological differences are selected or induced by environmental differences.

The findings concerning the numbers of pore-pairs in the petals of specimens from the four populations studied in this respect are puzzling in view of Durham's (1955) idea that the older specimens of comparable size would have more plates in the petals and in view of the aforementioned idea that the older specimens would have heavier tests. The fact that the specimens from Crow Neck are heaviest would indicate that they are slow growing, and their having the smallest numbers of pore-pairs in the petals would indicate that they are growing rapidly. Thus, it appears that until studies have been made in which the ages or growth-rates characteristic of populations are definitely determined, test weight and numbers of pore-pairs in the petals must be considered as independent of each other and neither should be considered as having a proven relationship to growth rate.

Summary

1. The widespread occurrence of skeletal variation in echinoids is indicated.

2. Variation in respect to several characteristics of the test has been studied in the sand dollar *Echinarachnius parma* (Lamarck) as it occurs in a number of New England localities.

3. Evidence is presented that indicates a tendency for these animals to produce tests longer than wide when living in flowing water and wider than long when living on surf-swept beaches.

4. In this species, as Raup (1958) reported earlier for *Dendraster* on our west coast, tests tend to be heavier at comparable sizes in populations living in colder water than those of warmer localities.

5. Populations vary from one another in numbers of pore-pairs in the petaloid areas of the ambulacra of individuals at comparable sizes, but no consistent correlations with environmental factors have been detected.

LITERATURE CITED

BARLOW, G. W., 1961. Causes and significance of morphological variation in fishes. *Systematic Zool.*, **10**: 105–117.

CLARK, H. L., 1935. Some new Echinoderms from California. *Ann. Mag. Nat. Hist., ser. 10*, **15**: 120–129.

CLARK, H. L., 1948. A report on the Echini of the warmer Eastern Pacific, based on the collections of the Velero III. *Allan Hancock Pacific Exped.*, **8**(5): 225–351 (plates 35–71).

DURHAM, J. W., 1955. Classification of Clypeasteroid Echinoids. *U. of Calif. Publ. Geol. Sci.*, **31**(4): 73–198 + frontispiece and plates 3 and 4.

GRANT, U. S., IV, AND L. G. HERTLEIN, 1938. The west American Cenozoic Echinoidea. U. Calif. Los Angeles Publ., Math. Phy. Sci., 225 pp. + 30 plates.

JACKSON, R. T., 1912. Phylogeny of the Echini, with a revision of Palaeozoic species. *Mem. Boston Soc. Nat. Hist.*, 7: 491 pp. + 76 plates.

JACKSON, R. T., 1914. Studies of Jamaica Echini. *Pap. Tortugas Lab. (Publ. No. 182 Carn. Inst.)*, **5**: 139–162.

JACKSON, R. T., 1927. Studies of *Arbacia punctulata* and allies and of nonpentamerous Echini. *Mem. Boston Soc. Nat. Hist.*, **8**(4): 433–565.

KERMACK, K. A., 1954. A biometrical study of *Micraster coranguinum* and *M. (Isomicraster) senonensis*. *Phil. Trans. Royal Soc. London*, **237**(B): 375–428.

KONGIEL, R., 1938. Rozważania nad zmiennościf jeżowcow. (Considerations on the variability of Echinoidea.) *Annu. Soc. geol. Pologne*, **13**: 194–250. (In Polish with French summary and legends for figures and tables. English translation OTS 60-21506 available from the Office of Technical Services, U. S. Department of Commerce, Washington 25, D. C.)

MACGINITIE, G. E., AND N. MACGINITIE, 1949. Natural History of Marine Animals. McGraw-Hill, New York, London, Toronto, 473 pp.

MORTENSEN, T., 1948. A monograph of the Echinoidea (vol. 4, part 2) Clypeastroida. C. A. Reitzel, Copenhagen, 471 pp. + 72 plates.

NICHOLS, D., 1959a. Changes in the chalk heart-urchin *Micraster* interpreted in relation to living forms. *Phil. Trans. Roy. Soc. London*, **242B**: 347–437.

NICHOLS, D., 1959b. Mode of life and taxonomy in irregular sea-urchins. Systematics Assoc. Publ., No. 3, pp. 61–80, 7 figs.

NICHOLS, D., 1962. Differential selection in populations of a heart-urchin. Systematics Assoc. Publ., No. 4, pp. 105–118, 8 figs.

RAUP, D. M., 1957. Classification and morphological variation in the genus *Dendraster*. Doctoral thesis submitted to the Division of Geological Science, Harvard Univ., 159 pp. + 24 pls.

RAUP, D. M., 1958. The relation between water temperature and morphology in *Dendraster*. *J. Geol.*, **66**(6): 668–677.

SHIH, C. Y., 1937. Die Abhängigkeit der Grosse und Schalendicke mariner Mollusken von der Temperatur und dem Salzgehalt des Wassers. Sitz. Ges. naturf. Fr. Berlin, pp. 238–287.

SWAN, E. F., 1952. The growth of the clam *Mya arenaria* as affected by the substratum. *Ecology*, **33**(4): 530–534.

SWAN, E. F., 1962. Evidence suggesting the existence of two species of *Strongylocentrotus* (Echinoidea) in the Northwest Atlantic. *Canad. J. Zool.*, **40**: 1211–1222.

U. S. DEPARTMENT OF COMMERCE, COAST AND GEODETIC SURVEY, 1951. Surface water temperatures at tide stations, Atlantic Coast North and South America. Special Publ. No. 278 Revised (1951) Edition. U. S. Government Printing Office, Washington; 57 pp.

VASSEUR, E., 1952. Geographic variation in the Norwegian sea urchins, *Strongylocentrotus droebachiensis* and *S. pallidus*. *Evolution*, **6**: 87–100.